# SILURIAN ODONTOPLEURID TRILOBITES FROM SWEDEN, ESTONIA, AND LATVIA

*by* DAVID L. BRUTON

ABSTRACT. All of the presently known Silurian odontopleurid material from Sweden has been revised along with recently collected material from Estonia and Latvia. For the first time photographs are given of the holotypes of *Odontopleura ovata* Emmrich and *Leonaspis mutica* (Emmrich). Examination of the latter shows that it is specifically distinct from the Swedish species *L. marklini* (Angelin) and the British species *L. coronata* (Salter). *Acidaspis lughesi* Lake is considered to be a synonym of *O. ovata*. The new genus *Anacaenaspis* (type species *A. gotlandensis* gen. et sp. nov.) is established for specimens which differ from *Acidaspis* Murchison in lacking the stout occipital spine. The holotype of '*Acidaspis*' *emarginata* Schmidt is refigured and has been assigned to *Anacaenaspis*. Newly described are two species of *Leonaspis*, *L. varbolensis* from the lowermost Llandovery of Estonia and Latvia, and *L. muldensis* from the uppermost Wenlock of Gotland. A previous record of the Bohemian species *Miraspis mira* (Barrande) in the Silurian of Scania has not been confirmed and it appears likely that all the material belongs to *M. cardiolarum* (Hede). Many of the specimens have been illustrated with the aid of stereoscopic photographs.

THE Island of Gotland has attracted many palaeontologists to its shores and large collections of Silurian fossils have been made. Angelin (1854) in his 'Palaeontologia Scandinavica' illustrated the largest single collection of Silurian odontopleurids from Gotland but, unfortunately, his descriptions were all too brief and the stratigraphic locations are vague. Earlier, Lovén (1845) described specimens of *Leonaspis crenata* (Emmrich) in great detail, and later Lindström (1885) supplemented many of Angelin's descriptions with the aid of newly collected material.

From the less abundant collecting areas in Västergötland, Dalman (1828) described as *Calymene? centrina* (= *Leonaspis centrina*) one of the first odontopleurid trilobites to appear in the literature. More recently Hede (1915) described specimens from the Colonus Shale of Scania.

Outside Sweden, principally in Germany, Emmrich (1839; 1844–5), Beyrich (1846), Roemer (1885), and Wigand (1888) illustrated several specimens obtained from erratics of Graptolithengestein. These erratics, derived from the sub-Baltic outcrops of this horizon, were deposited during the penultimate (Saale) glaciation along the Pomeranian coast and as far east as Silesia. Emmrich's (1839) classic 'Dissertatio de Trilobitis', contains the description and illustration of *Odontopleura ovata* the type species of the genus *Odontopleura*. Schmidt (1885) described one odontopleurid species from the Silurian of Estonia.

In 1963 it was my good fortune to be able to study the large collection of Silurian odontopleurids from Gotland at the Natural History Museum, Stockholm, and a smaller collection at the University of Uppsala. Specimens from Lund and the types of Emmrich and Beyrich from the Humboldt University, East Berlin, were obtained on loan and were examined at Uppsala.

A visit to the Soviet Union in April and May 1965, enabled me to examine and photograph material recently obtained from borings which penetrated the Silurian succession in Latvia and on the Estonian Baltic Islands of Saaremaa and this, and other material from Estonia, is described in this paper.

[Palaeontology, Vol. 10, Part 2, 1967, pp. 214–44, pls. 30–36]

The terminology used in this paper is the same as that employed in previous publications (Bruton, 1965; 1966*a*, *b*). All specimens were lightly coated with ammonium chloride before photographing and, except where stated, were taken by the author. The isolated specimens obtained from the Mulde Marl were all mounted on pins and these have been blacked out where they showed on the print; otherwise the photographs have not been retouched. The stereoscopic pairs were made in the same manner as outlined in a previous publication (Bruton 1965, p. 344).

*Acknowledgements.* I am most grateful to Professor E. Jarvik, Swedish Museum of Natural History (Naturhistoriska riksmuseet, paleozoologiska avd., RM), Stockholm, for allowing me to work at the Museum, and to Dr. Harry Mutvei for arranging a subsequent loan of the material. The following people also kindly allowed me to borrow material for study: Professor Gerhard Regnéll, Paleontological Museum, University of Lund (LM), and Professor Per Thorslund, Paleontological Museum, University of Uppsala (UM). The types of Emmrich and Beyrich were borrowed on my behalf by Dr. Anders Martinsson, and were sent by Dr. Hermann Jaeger, Geological–Paleontological Museum, Humboldt University, East Berlin (HU). Dr. Ralph Männil, Geological Institute, Estonian Academy of Sciences, Tallinn (EA) generously made available to me all the Silurian material from Latvia and Estonia. A type specimen from the Schmidt Collection at the Karpinsky Museum, Leningrad (KPL), was made available for study, and Dr. Z. A. Maksimova, Central Geological Museum, Leningrad (CGML), allowed me to study comparative material from Siberia. The initials following the name of an institute are those used subsequently in referring to specimens.

At Uppsala, Professor Thorslund graciously afforded me the facilities of his Institute, Mr. Nils Hjorth made the photographs of the specimens from Berlin, and Mr. Eric Ståhl drew the text-figures. Where possible, Dr. Martinsson has kindly given advice on the stratigraphic location of the specimens and identified many of the lithologies and has also read the manuscript. Professor P. C. Sylvester-Bradley and Dr. Valdar Jaanusson have both been a constant source of encouragement throughout the preparation of this paper.

My work in Sweden was made possible with the help of an S.R.C. studentship and the visit to the Soviet Union was partly financed by the University of Leicester and partly by the British Council. To all these bodies I extend my sincere thanks.

## STRATIGRAPHY

Regnéll and Hede (1960) have recently summarized the Silurian succession in Scania and Gotland, and Wærn (1948) has dealt with the succession of Västergötland.

In Scania, the Colonus Shale (see Hede, 1915, p. 54; Regnéll and Hede, 1960, p. 29) contains *Monograptus nilssoni* and *M. scanicus* thus indicating a Lower Ludlow age. The presence of *M. vulgaris* below and *M. tumescens–M. leintwardinesis* above, has not been confirmed.

On Gotland, the scarcity of graptolites or the infrequent occurrence of long-ranging forms in what is a thick predominantly shelly succession, makes correlation with the British succession only approximate. After a detailed appraisal of the graptolites recorded from Gotland, Hede (1942, p. 226) concluded that the Upper Visby Marl is equivalent to the Upper Llandovery and perhaps basal Wenlock, the Högklint Beds have a time equivalence with the Lower Wenlock, the Slite group is, in part, equal to the Upper Wenlock (zone of *Cyrtograptus ellesi*), the Mulde Marl possibly represents a transition from the Upper Wenlock (zone of *C. lundgreni*) to the lowermost Ludlow, and the Hemse Group corresponds well with the Lower Ludlow (*M. nilssoni*).

Martinsson (1963*b*, p. 540) has shown that the submarine exposures of Gotland may extend above the zone of *M. nilssoni* or even to the top of the British Silurian succession

as indicated by the south-western continuation of a more argillaceous facies, the Graptolithengestein, between the island and the neighbourhood of the North Mid-Sea Bank (see Martinsson 1963*a*, pp. 8–9, fig. 3).

In Västergötland, Wærn (1948, pp. 460–1) showed that at Kinnekulle, the so-called zone of *Acidaspis centrina* and *Climacograptus scalaris* corresponds to several lowermost Llandoverian graptolite zones.

A summary of the Silurian succession in Estonia is given by Aaloe *et al.* (1960, pp. 28–39).

## SYSTEMATIC DESCRIPTIONS

### Family ODONTOPLEURIDAE Burmeister 1843
### Subfamily ODONTOPLEURINAE Burmeister 1843
### (= Odontopleuridae of Prantl and Přibyl 1949)

### Genus ODONTOPLEURA Emmrich 1839

Type species: *Odontopleura ovata* Emmrich 1839.

A diagnosis of the genus has recently been given by Whittington 1956*a*, p. 195.

### *Odontopleura ovata* Emmrich, 1839

Plate 30, fig. 1

1839 *Odontopleura ovata* Emmrich, p. 53, pl. 1, fig. 3.
1843 *Odontopleura ovata* Emmrich; Burmeister, p. 72, pl. 2, fig. 11.
1844 *Odontopleura bispinosa* Emmrich, p. 17, pl. 1, fig. 12.
1845 *Odontopleura bispinosa* Emmrich; Emmrich, p. 44, pl. 1, fig. 12.
1846 *Odontopleura ovata* Emmrich; Beyrich, p. 18, pl. 3, fig. 1.
1846 *Odontopleura ovata* Emmrich; M'Coy, p. 46.
1846 *Odontopleura Prevosti* Barrande, p. 56.
1846 *Odontopleura ovata* Emmrich; Burmeister, p. 62, pl. 2, fig. 11.
1847 *Odontopleura Prevosti* Barrande; Hawle and Corda, p. 148.
1847 *Odontopleura Bronni* Hawle and Corda, p. 150.
1847 *Odontopleura Neumanni* Hawle and Corda, p. 151.
1847 *Odontopleura tenuicornis* Hawle and Corda, p. 155.
1852 *Acidaspis Prevosti* (Barrande) Barrande, p. 739, pl. 39, figs. 33–41.
1883 *Acidaspis Prevosti* (Barrande); Novák, p. 41, pl. 10, figs. 12–14.

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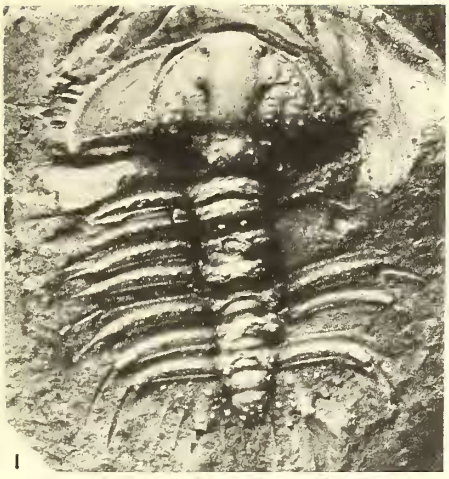
EXPLANATION OF PLATE 30

Fig. 1. *Odontopleura ovata* Emmrich, Graptolithengestein (Upper Wenlock–Lower Ludlow) erratic, Nieder-Kunzendorf, Silesia. Holotype, HU k162, original of Emmrich 1839, pl. 1, fig. 3, dorsal view, ×3.

Figs. 2–8. *Leonaspis marklini* (Angelin). 2, 4, Anterior view and dorsal stereograph of internal mould of cranidium, RM Ar 6340, ×5. ?Slite or Halla Beds (Upper Wenlock), Stora Karlsö, Gotland. 3, Incomplete internal mould of pygidium, UM G819, ×6. ?Halla Beds, Lilla Karlsö, Gotland. 5, Dorsal stereograph of partly exfoliated pygidium, RM Ar 30861, ×4¼. Horizon unknown ('Visby b'), Gotland. 6, Dorsal view of exfoliated exoskeleton lacking free cheeks, RM Ar 6339, ×1½. ?Mulde Beds (Upper Wenlock), Djupvik in Eksta, Gotland. 7, Holotype, UM G4, original of Angelin 1854, pl. 22, fig. 13, latex cast of external mould of an incomplete thorax and pygidium, ×3. Mulde Beds, Gannarve in Fröjel, Gotland. 8, Oblique dorsal view of almost complete isolated free cheek, RM 47406, ×7. Mulde Beds, Djupvik in Eksta, Gotland.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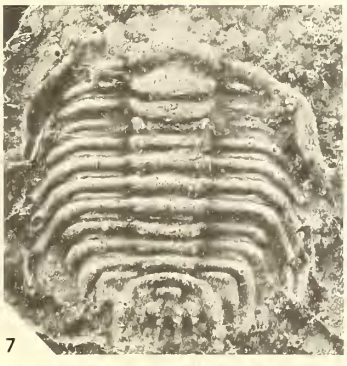
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1885 *Odontopleura ovata* Emmrich; Roemer, p. 129, pl. 10, fig. 7.
?1888 *Odontopleura* cfr. *ovata* Emmrich; Wigand, p. 99, pl. 10, figs. 21, 22.
1892 *Odontopleura ovata* Emmrich; Clarke, p. 7, pl. 3, fig. 1.
1896 *Acidaspis Hughesi* [Salter MS.]; Lake, p. 242, pl. 8, figs. 4, 5.
1901 *Odontopleura ovata* Emmrich; Van Ingen, p. 37, fig. 3.
1916 *Odontopleura ovata* Emmrich; Raymond, p. 136.
1925 *Odontopleura ovata* Emmrich; Warburg, p. 236.
1925 *Ceratocephala* (*Odontopleura*) *ovata* (Emmrich); R. and E. Richter, p. 126.
1925 *Acidaspis* (*Leonaspis*) *ovata* (Emmrich); Reed, p. 426.
1926 *Odontopleura ovata* Emmrich; R. Richter, p. 253.
1930 *Odontopleura ovata* Emmrich; Gaertner, p. 196, pl. 24, fig. 11.
1933 *Odontopleura ovata* Emmrich; Warburg, p. 2.
1949 *Odontopleura ovata* Emmrich; Prantl and Přibyl, p. 138, pl. 1, figs. 1–4; pl. 7, figs. 1–3; text-fig. p. 126.
1953 *Odontopleura ovata* Emmrich; Hupé, p. 231, fig. 134.
1953 *Odontopleura ovata* Emmrich; Přibyl, p. 49.
1956*a* *Odontopleura ovata* Emmrich; Whittington, p. 196, fig. 4.
1957 *Odontopleura ovata* Emmrich; Tomczykowa, p. 94 (133), figs. 5*a–d*, pl. 2, figs. 3–7.
1958 *Odontopleura ovata* Emmrich; Prantl and Vaněk, tab. 11 (39).
1959 *Odontopleura ovata* Emmrich; Whittington *in* Moore, p. 0504–5, fig. 1.
1960 *Odontopleura ovata* Emmrich; Maksimova, pp. 156–7, fig. 359.

*Holotype*. The incomplete cephalon, part thorax, and pygidium (HU k162) figured by Emmrich 1839, pl. 1, fig. 3 and refigured herein as Plate 30, fig. 1.

*Locality*. The holotype was found in erratics at Nieder-Kunzendorf, Silesia.

*Horizon*. Upper Wenlock–Lower Ludlow Graptolithengestein (erratic).

*Dimensions*. Cranidium: length (sag.) 6 mm.; width between palpebral lobes 7·5 mm.; free cheek: maximum transverse width 4 mm.; maximum length 3·5 mm.; pygidium: width 9·5 mm., length 2·5 mm.

*Description*. The undistorted holotype (Pl. 30, fig. 1) still retains much of the exoskeleton and consists of a cephalon, lacking the right free cheek, lying near articulated parts of seven thoracic segments and a pygidium.

Cephalon wide transversely and semi-elliptical in outline; cranidium moderately convex. Median glabellar lobe tapering slightly backwards from about half length (sag.); frontal lobe expanding laterally and sloping steeply downwards to anterior border furrow. Occipital ring with long (sag.) and moderately convex median portion separated from remainder of glabella by abrupt change of slope. Small occipital lobe outlined by deep lateral part of occipital furrow beneath L1 and the outwardly curved termination of the longitudinal furrow. Occipital ring with large median granule placed at the base of paired occipital spines (broken and missing on specimen). Two pairs lateral glabellar lobes, L1 the larger, elliptical in outline with longest axis slightly oblique to sagittal line; L2 suboval. S1 inclined at about 45°, curved backwards and very deep adjacent to the median lobe; S2 more oblique and slot-like. Longitudinal furrow broad and shallow especially across inner end of L1. Dorsal furrow almost absent at the outer end of L1 so that here the lobe and the adjacent fixed cheek are confluent. Eye ridge narrow, convex, curved outward and backwards from the lateral expansion of the frontal lobe. Palpebral lobe not preserved, but the broken base indicates that the eye was placed opposite the outer end of the occipital furrow. Fixed cheek widest inside the eye from where it slopes steeply down to the posterior margin, gently convex (tr.), sloping outwards from the dorsal furrow to the eye ridge. Course of the anterior facial suture

defined by a sutural ridge which diverges from the eye ridge opposite the inner end of S1, curves gently forwards and crosses the obliquely directed anterior margin at a position just outside of an exsagittal line drawn through the midpart of the fixed cheek. Posterior suture long, directed outwards and downwards at right angles to the anterior sutural course, curving backwards inside the base of the librigenal spine. Posterior border of cranidium with rolled margin and straight, moderately deep border furrow. Free cheek with length of anterior and posterior sutures about equal. Border narrow, convex, widening towards the librigenal angle. Librigenal spine not present on the holotype, but a cheek lying nearby shows that the spine is at least as long as the cephalon and that it tapers backwards, incurving distally. Cheek margin with at least fifteen very closely spaced fringing spines which decrease in length towards the anterior suture and terminate immediately in front of an exsagittal line drawn through the palpebral lobe. Cheek surface flat to gently sloping downwards from the eye to the border. Fixed cheek with coarse blunt granules between which is a finer granulation; the latter occurs also on the fronto-median and lateral glabellar lobes. Paired granules flank the median occipital tubercle; free cheek finely granulated.

Only parts of seven thoracic segments are known. Rachis strongly convex, occupying about one-half width of segment; rachial ring with slightly raised median band connected to the principal pleural ridge of the segment. Principal pleural ridge broad, weakly convex, and gently curved convexly forward. At the fulcrum the ridge is slightly swollen but it rapidly tapers outwards into the principal pleural spine. Latter very short on anterior segments and directed straight outwards and downwards, while on the posterior segments the spine is longer and curved progressively backwards. Anterior accessory area shallow and smooth with a raised granulated anterior ridge which becomes flattened at the distal end with the production of an articulating process and a slim anterior spine. Posterior margin of segment with very narrow (exs.) flange. Principal pleural ridge with conspicuous granules positioned (1) at the fulcrum, (2) one-half, and (3) one-third (from rachis) pleural width; between these larger granules there occur respectively, on every segment, a smaller pair of granules and a smaller single granule. Rachis with large paired central tubercles and smaller granules on the lateral shoulder.

Pygidium about three times as wide as long with rachis of two rings and short lower terminal portion which almost reaches the posterior border. Dorsal furrow shallow alongside rings but very deep at the outer end of the separating furrow. Pleural ridge short and curved sharply backwards from alongside first rachial ring, slightly swollen at border. Major border spines incomplete. Between major spines, four very short, slim secondary spines which are unequally spaced. Outside the major spine are four anterior secondary spines (the outermost spine is not visible on the photograph (Pl. 30, fig. 1) since it is partly overlapped by the principal pleural spine of the preceding segment). Pleural area flat to gently sloping towards the margin; border furrow absent. Rachis with paired tubercles on each ring and paired tubercles on the pleural ridge, one at base of major spine, the other alongside first rachial ring. Remainder of pleural area with odd smaller granules and very fine granulation between.

*Discussion.* Plate 30, fig. 1, is the first photograph of the holotype to have been published. Emmrich's figure gives a fairly accurate portrayal of the specimen except that it is laterally inverted. The specimen is of a moulted thorax and pygidium lying behind a

cephalon. Although only parts of seven (possibly the remnant of an eighth) segments are present (as noted by Emmrich in the original description), the dimensions of the specimen indicate that this is a holaspid, and not a juvenile individual as believed by Prantl and Přibyl (1949, p. 139). It seems likely that the first two segments were lost during ecdysis.

The later figures of the holotype given by Burmeister (1843), and Emmrich (1844–5) are very idealized and the omission of the occipital spines led to further misinterpretations of this species by many authors (for full discussion see Prantl and Přibyl 1949, pp. 136–7). Emmrich (1844) quite unnecessarily changed the name of his species, but as outlined by M'Coy (1846, p. 46), the specific name *ovata* has priority.

Gaertner (1930, p. 197) examined the holotype and showed quite correctly that the species described by Barrande as *Odontopleura prevosti* from the Bohemian Silurian (Wenlock–Lower Ludlow), is the same as *O. ovata*. Moreover, I have examined specimens of *Acidaspis hughesi* taken from the British Upper Wenlock–Lower Ludlow and consider that they are the same as *O. ovata*. The British and Bohemian specimens are to be described by me in forthcoming papers (in manuscript).

## Genus LEONASPIS R. and E. Richter 1917

[= *Acanthaloma* Conrad 1840; suppressed, 1957, I.C.Z.N. **17** (20), pp. 361–76, OPINION 498, after recommendations by Whittington (1956*c*)].

*Type species.* *Odontopleura leonhardi* Barrande 1846.

A recent diagnosis of the genus has been given by Whittington (1956*a*, p. 206).

### *Leonaspis marklini* (Angelin, 1854)

Plate 30, figs. 2–8; Plate 31, figs. 1–3

1854 *Acidaspis Marklini* Angelin, p. 38, pl. 22, fig. 13.
? 1854 *Acidaspis multicuspis* Angelin, p. 37, pl. 22, fig. 12.
1885 *Acidaspis marklini* Angelin; Lindström, p. 54, pl. 13, figs. 8, 15; pl. 16, fig. 10.
? 1888 *Acidaspis mutica* (Emmrich); Wigand, p. 93, pl. 10, figs. 19–20.
1896 *Acidaspis marklini* Angelin; Lake, p. 238.
*non* 1907 *Acidaspis marklini* Angelin; Schmidt, p. 22 [= *Anacaenaspis emarginata* (Schmidt)].
*non* 1938 *Leonaspis marklini* (Angelin); Whittard, p. 108, pl. 3, fig. 14 [= ? *Leonaspis varbolensis* sp. nov.].

*Holotype.* The incomplete external mould of a cephalon with thorax and pygidium (UM G4), figured by Angelin 1854, pl. 22, fig. 13. A latex cast of the specimen is figured herein as Plate 30, fig. 7.

*Type localities.* Cape of Skäret below Gannarve in Fröjel, Lilla Karlsö, Stora Karlsö, Djupvik in Eksta, and Visby, Gotland.

*Horizon.* Upper Wenlock–Lower Ludlow, Halla Beds, and Mulde Beds.

*Material.* The types of Lindström (RM Ar 6639–40), two free cheeks (RM Ar 47404; 47406), one cranidium and pygidium (UM G 819; 820), and one pygidium (RM Ar 30861), all figured, plus several pygidia and free cheeks in the collections at the Riksmuseum, Stockholm.

*Description.* Cranidium (Pl. 30, fig. 4; Pl. 31, fig. 3) trapezoidal in outline, maximum width measured between palpebral lobes slightly greater than sagittal length. Median

glabellar lobe sloping very gently forwards from occipital furrow; frontal lobe with a rounded anterior margin which slopes steeply down to the anterior border furrow. Occipital ring gently convex with median tubercle positioned inside posterior margin. Median tubercle (Pl. 31, fig. 3) with four tiny depressions (= median occipital organ of Whittington 1965, p. 297) arranged to outline the corners of a square. Small low occipital lobe developed, its convexity outlined by the deep outer part of occipital furrow beneath L1 and a slight posterior extension of the longitudinal glabellar furrow. Median part of occipital furrow broad and shallow. Two pairs lateral glabellar lobes, L1 the larger, oval in outline, slightly pointed at the outer end; L2 oval, about half the size of L1. Longitudinal furrow a broad, smooth, shallow area marking a slight change of slope between the lateral lobes and adjacent parts of the median lobe. S1 deep and oblique to the sagittal line at outer end, almost transverse between the lobes, then curved backwards and very deep adjacent to the median lobe; S2 narrow, slot-like, outlining the lateral expansion of frontal-glabellar lobe. Eye ridge (Pl. 30, fig. 2) moderately broad, convex, curving outwards and backwards from a depressed flattened area at side of frontal lobe. Palpebral lobe (Pl. 31, fig. 3) positioned far back on the fixed cheek so that a transverse line drawn through the midpoint is level with the base of L1. Palpebral lobe directed upwards and slightly backwards with an outer curved lip, palpebral furrow very deep at base of lobe. Fixed cheek widest posteriorly where it slopes vertically down to the posterior border furrow, narrowing anteriorly and becoming diminished between outer part of L2 and the furrow along the inner edge of the eye ridge. Dorsal furrow shallow to lacking anteriorly but deeper around the outer posterior part of L1. Course of anterior branch of facial suture defined by a sutural ridge which diverges from eye ridge opposite the outer end of S1, runs forward, then makes a sharp turn and converges towards the straight anterior border. Transverse width between anterior sutures slightly less than the maximum width of the cranidium. Antero-lateral part of the border flat but very deep and slot-like at the inner corner and beneath the eye ridge. Posterior branch of facial suture directed outwards at right angles to anterior suture and curved sharply backwards inside base of swollen librigenal spine. Posterior margin straight with deep furrow. Fronto-median lobe (Pl. 30, fig. 2), lateral lobes, fixed cheek, and occipital ring with large blunt tubercles between which are smaller granules; eye ridge with single row of smaller tubercles.

No cranidium has been found with free cheeks attached but the two cheeks (Pl. 30, fig. 8; Pl. 31, figs. 1–2) found amongst washings from the Mulde Marl are thought to belong here on account of their proportions and the similarity of the exoskeletal ornament with that of the cranidium. Border near anterior suture with narrow raised ridge which becomes less obvious towards the librigenal spine; border wide and flattened. Librigenal spine swollen at the base, directed outwards into a very short stumpy spine which is slightly curved at its distal end. Cheek border with at least ten short, stout spines directed outwards and downwards from the lower margin. Cheek surface concave inside margin and then sloping upwards to eye lobe; beneath latter, cheek slopes steeply down to short furrow inside the posterior sutural ridge. On ventral side (Pl. 31, fig. 2), doublure forming a wide, smooth, curved band which slopes rather steeply inwards. At the anterior suture is a short outward extension of the doublure (Pl. 30, fig. 8) which is related to the position of the antennular notch (see Whittington 1956*a*, p. 173); posteriorly, a short notch with a raised anterior edge occurs inside the base of the librigenal spine (Pl. 31, fig. 2). Cheek

surfaces smooth or with scattered granules; base of librigenal spine with large blunt tubercles; ventral surface of spine and doublure minutely granulated.

Hypostoma unknown.

Thorax (Pl. 30, fig. 6) with ten segments. Rachis wide (tr.), narrow (sag.), tapering posteriorly and occupying about one-half the total width of the segment. Articulating half-ring as wide as rachis and with gently curved anterior margin; articulating furrow narrow and deep laterally, becoming wider and shallower sagittally. Pleura horizontal and crossed by slightly inclined narrow pleural furrow dividing pleura into broad (exs.), gently convex, principal pleural ridge and a narrower anterior accessory ridge with short anterior pleural spine present only on the posterior seven segments; posterior margin straight with small flange. First three segments shortened transversely, the first two faceted and without pleural spines, the third segment with very short anterior and principal pleural spines. Principal pleural ridge on remaining seven segments swollen at the fulcrum and produced into a long principal pleural spine which is directed downwards and outwards and then curved slightly upwards and backwards at the distal end. Every pleura with a conspicuous granule at the fulcrum and the first nine segments with a second granule at half pleural width; some segments have a smaller third granule near the dorsal furrow. Rachis with a staggered row of small granules. Pleural terminations on first segments finely granular, principal pleural spines on remaining segments with granules produced into small thorn-like projections.

Pygidium (Pl. 30, fig. 6) excluding spines approximately rectangular with straight anterior margin and sloping lateral corners. Rachis with two rings and a lower triangular terminal portion which reaches the wide posterior border but is not totally circumscribed by the deep dorsal and border furrows. First ring strongly convex, separated by deep ring furrow from lower second ring. Pleural ridge flat to gently convex, curved backwards to the enlarged part of the border at the base of the major spine. Latter divergent but curved slightly upwards and inwards distally; length at least twice that of pygidium. Between the major spines are four shorter and tapered posterior secondary spines. A single anterior secondary spine occurs outside the major spine and inside a short articulating process. Pleural area smooth and gently concave between the anterior and posterior border and pleural ridge. Major and posterior border spines with a conspicuous granule at the base and the remainder of the spine very closely granular. Rachis with at least two granules on each ring and smaller granules between. The pygidium (Pl. 30, fig. 3) found in association with the cranidium (Pl. 31, fig. 3) from the ?Halla Beds, Lilla Karlsö, differs slightly from that described above in that the border spines appear to be more slender and round in cross-section and the granulation is less conspicuous. These are slight differences and probably reflect the mode of preservation. The possibility that this may be a dimorphic difference should not be excluded. The same applies to the pygidium (Pl. 30, fig. 5) from Visby.

*Discussion.* The holotype of *Leonaspis marklini* (Pl. 30, fig. 7) from Gannarve in Fröjel, is a poorly preserved external mould with thorax and pygidium more or less complete and parts of the occipital ring and librigenal spine just visible. Angelin's description is very inadequate and the exact stratigraphic location is not known although the lithology of the matrix suggests that the specimen came from within the Mulde Beds. As far as can be judged, details of the thorax and pygidium are identical to the well-preserved

specimen (Pl. 30, fig. 6) which was illustrated by Lindström (1885, pl. 13, fig. 15) from the locality of Djupvik in Eksta. The stratigraphic location of this specimen is also in doubt but in the matrix surrounding the specimen are two fragments of cruminae and one young moult stage of the ostracode *Craspedobolbina* cf. *percurrens* (seen in the bottom right-hand corner of Pl. 30, fig. 6) which indicates an age of not younger than the Hemse Beds. *C. percurrens* is found commonly in the Mulde Marl and Dr. Anders Martinsson (verbal communication) believes that Lindström's specimen most likely came from this horizon. Thus this specimen has been used to redefine the species *Leonaspis marklini* (Angelin).

Lindström (1885, pl. 16, fig. 10) regarded a second cranidium (Pl. 30, fig. 4) from Stora Karlsö, as being the original of Angelin's *Acidaspis multicuspis* and this he indentified with *marklini*. However, the late Dr. Elsa Warburg (see footnote, Whittard 1938, p. 109) was of the opinion that this specimen figured by Lindström was not Angelin's type and that the type had been lost. I subscribe to this view, for it is impossible to recognize this specimen as being the one used for the inadequate figure given by Angelin (1854, pl. 22, fig. 12).

Lake (1896, p. 238) after examining this specimen and another figured by Lindström as *A. marklini*, considered that they were identical with the earlier described British Wenlockian species *Leonaspis coronata* (Salter 1853) and possibly also *L. mutica* (Emmrich 1844) from the Silurian Graptolithengestein erratics of Silesia. However, I agree with Whittard (1938, p. 110) that *L. coronata* and *L. marklini* are different. *L. marklini* differs from *L. coronata* (cf. Whittington 1956*b*, pl. 59, fig. 12) in having (1) a more convex and stronger occipital ring, (2) a wider and more strongly inflated posterior part of the fixed cheek, (3) a longer (sag.) more expanded and rounded frontal lobe, and (4) a more coarsely granular exoskeleton. The free cheek thought to belong to *L. marklini* differs from that of *L. coronata* in having a much shorter and stumpy librigenal spine. The distinguishing features between *L. marklini* and *L. mutica* are given on page 223.

## *Leonaspis mutica* (Emmrich, 1844)

Plate 31, figs 4–9; Plate 32, figs. 1–2

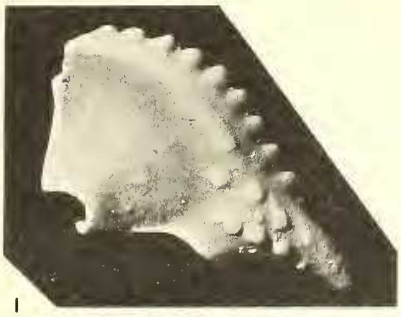
1844 *Odontopleura mutica* Emmrich, p. 17.
1845 *Odontopleura mutica* Emmrich, p. 44.
1846 *Odontopleura mutica*; Beyrich, p. 19, pl. 3, fig. 3.
1852 *Acidaspis mutica* (Emmrich); Barrande, p. 703.
1885 *Acidaspis mutica* (Emmrich); Roemer, p. 129, pl. 10, figs. 8*a–c*.

EXPLANATION OF PLATE 31

Figs. 1–3. *Leonaspis marklini* (Angelin). 1, 2, Dorsal and ventral stereographs of a complete isolated free cheek, RM Ar 47404, ×12½. Mulde Beds, Djupvik in Eksta, Gotland. 3, Dorsal view of incomplete cranidium, UM G820, showing the median occipital organ, ×5½. ?Halla Beds, Lilla Karlsö, Gotland.

Figs. 4–9. *Leonaspis mutica* (Emmrich). 4, Dorsal view of cranidium, EA Tr 2336/1, ×4. Jaani Stage ($J_1$)–upper Lower Wenlock–lower Upper Wenlock, level 303 m., Ohesaare boring, Island of Saaremaa, Estonia. 5, Free cheek with eye lobe attached, EA Tr. 2335/2, ×4. Same locality and horizon as fig. 4, level 311·80–90 m. 6, Pygidium, EA Tr. 2337, ×7. Level 307· 60–70 m. 7–9, Holotype, HU k195. Graptolithengestein erratic, Nieder-Kunzendorf, Silesia. 7, Dorsal view of the incomplete and exfoliated pygidium which is displaced relative to the length of the body, ×6. 8, Oblique view of the partly exfoliated cranidium, ×6. 9, Detail of the median occipital organ, ×30.

Figs. 7–9 taken by Mr. N. Hjorth.



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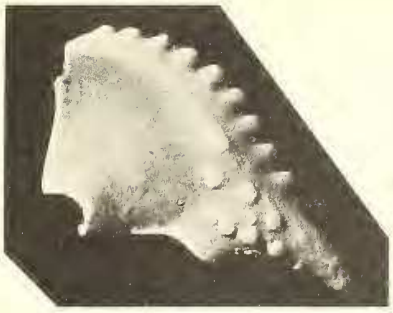

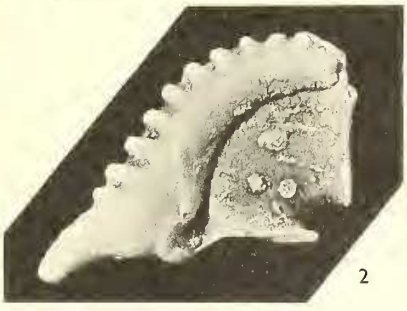

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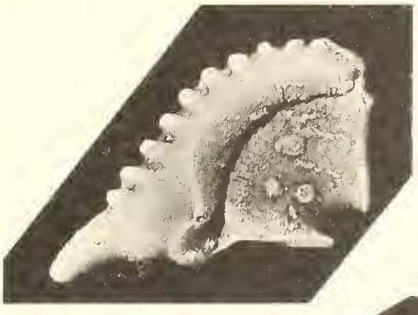

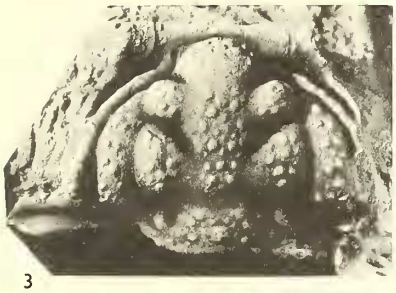

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BRUTON, Silurian odontopleurids

1885 *Acidaspis mutica* (Emmrich); Lindström, p. 55.
1896 *Acidaspis mutica* (Emmrich); Lake, p. 238.
*non* 1888 *Acidaspis mutica* (Emmrich); Wigand, p. 93, pl. 10, figs. 19–20 [= ?*Leonaspis marklini* (Angelin)].

*Holotype.* The partly enrolled and incomplete specimen (HU k195), figured Plate 31, figs. 7–9; Plate 32, figs. 1–2.

*Dimensions of holotype.* Cranidium: length (sag.) 5 mm.; width (between the palpebral lobes) approximately 6·5 mm.; pygidium: width 8 mm.; length 2·5 mm.

*Type locality.* The holotype was found in an erratic at Nieder-Kunzendorf, Silesia.

*Horizon.* Lower Ludlow Graptolithengestein erratic boulders.

*Material.* In addition to the holotype, one incomplete pygidium from the Beyrich Collection (HU k196), two cranidia, two free cheeks, and two pygidia (EA 2235/1–3; 2336/1–2; 2337) obtained from the 307·60 m.–311·84 m. levels of a boring made in the upper Lower Wenlock–lower Upper Wenlock, Jaani Stage ($J_1$) at Ohesaare, Island of Saaremaa, Estonia.

*Description.* The partly enrolled holotype (Pl. 32, fig. 1) still retains much of the exoskeleton on the cranidium but the remainder of the body is preserved as an internal mould. The left free cheek is displaced and lies at the side and below the cranidium (Pl. 32, fig. 2); the right free cheek is missing. Because of the similarity between *L. mutica* and *L. marklini*, a formal description is unnecessary. The features which distinguish *L. mutica* from *L. marklini* may be described as follows: Cranidium (Pl. 32, fig. 2; cf. Pl. 31, fig. 3; Pl. 31, fig. 4) with a shorter (sag.), flatter (tr.), and less inflated frontal glabellar lobe which slopes steeply down to the anterior border and furrow. L1 with more rounded anterior end and S1 shorter, curved sharply backwards adjacent to the median lobe, and not deeply incised between the lobes. Median portion of the occipital ring not strongly raised, occipital lobe only faintly outlined between the shallow lateral part of the occipital furrow and the posterior end of the longitudinal furrow. Anterior branch of the facial suture curving gently inwards and running outside and parallel to the eye ridge as far as the outer end of S2, then curving more strongly inwards. The outer area of the fixed cheek is therefore narrower and flatter and the lateral corner of the anterior border is rounded. The lateral border of the free cheek (Pl. 31, fig. 5) projects forwards alongside the anterior suture and there is a sharp angle between this projection and the first fringing spine. The narrow raised border becomes lower and less convex and dies out at the base of the librigenal spine. Latter (Pl. 31, fig. 5; Pl. 32, fig. 2) incomplete, but the base is broader and flatter than in *L. marklini* (cf. Pl. 30, fig. 8; Pl. 31, fig. 5) and is very finely granular. The whole of the exoskeleton of *L. mutica* is very finely granular in contrast to the coarse blunt tubercles of *L. marklini*. Both species have the median occipital organ and Plate 31, fig. 9 shows this structure of *L. mutica* in some detail.

Thorax (Pl. 31, fig. 7; Pl. 32, fig. 1) with only nine segments as opposed to ten in *L. marklini*. The first three segments are shortened transversally, the first two being faceted. Details of the pleural spines not known for the posterior segments.

Pygidium (Pl. 31, figs. 6–7) closer to that of *L. marklini* (Pl. 30, fig. 6) than the other pygidia (Pl. 30, figs. 3, 5), but differing from all three in that the rachis does not reach the posterior border furrow, and the terminal portion is indistinct to lacking below the second rachial ring. The border spines are broader and flatter and the major spine is more incurved. In addition to the larger granules on the posterior border and at the base of each spine, there is a second conspicuous granule on the spine itself.

*Discussion.* The holotype is from a Silurian erratic supposedly of the Graptolithgestein (Upper Wenlock–Lower Ludlow) horizon in the Baltic area. The new material, recently collected from an older horizon on the Baltic Island of Saaremaa, agrees very well with the holotype, suggesting that *L. mutica* either ranges from the upper Lower Wenlock–Lower Ludlow, or that the holotype comes from a lower horizon than was originally thought.

The holotype of *L. mutica* is almost certainly a holaspid, and the presence of only nine segments in the thorax is not an indication of immaturity. Now that the holotype has been examined, it is clear that *L. mutica* is different from *L. marklini* (cf. remarks by Lindström 1885, p. 55; Lake 1896, p. 238).

I have not seen the material figured by Roemer (1885) and Wigand (1888) and the figures given by these authors are not ideal. Wigand (1888, p. 98) noted that his specimens from the Graptolithengestein were more coarsely granular than *L. mutica*, which leads me to suspect that they might well be the same as *L. marklini*. Only examination of the material (if it still exists) would confirm this.

## *Leonaspis crenata* (Emmrich, 1844)

Plate 32, figs. 3–8; Plate 33, figs. 1–2, 5; Plate 34, figs. 1–2

1844 *Odontopleura crenata* Emmrich, p. 17.
1845 *Odontopleura crenata* Emmrich; Emmrich, p. 44.
1845 *Ceraurus crenatus* (Emmrich); Lovén, p. 47, pl. 1, figs. 6*a–b*.
1852 *Acidaspis crenata* (Emmrich); Barrande, pp. 697 and 700.
1854 *Acidaspis crenata* (Emmrich); Angelin, p. 34, pl. 21, figs. 6*a*, *b*.
1885 *Acidaspis crenata* (Emmrich); Lindström, p. 53.
1901 *Acidaspis crenata* (Emmrich); Lindström, p. 35, pl. 1, figs. 1–6.
1949 *Acanthaloma* (*A.*) *crenata* (Emmrich); Prantl and Přibyl, p. 162.
*non* 1896 *Acidaspis crenata* (Emmrich); Lake, p. 239, pl. 7, figs. 1–2 [= *Leonaspis* sp. nov.].

*Lectotype* (*here chosen*). The incomplete cephalon and part thorax (HU MB 1963/29/1), one of two syntypes from the Emmrich Collection. The specimen is figured herein as Plate 32, fig. 3.

*Other material.* The hypostoma (RM Ar 30816) figured by Lindström 1901, pl. 1, fig. 3, plus many partly complete and enrolled specimens, free cheeks, hypostomata and pygidia from the Riksmuseum, Stockholm. The following specimens are all figured, RM Ar 30806, 30809, 30813, 30816, 30824, and 31492.

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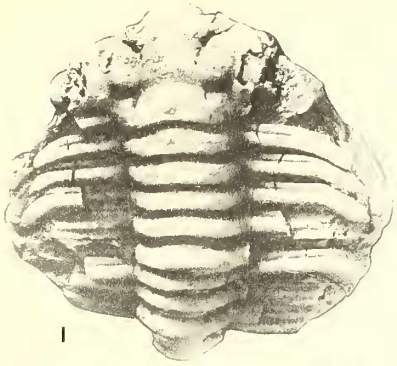
EXPLANATION OF PLATE 32

Figs. 1, 2. *Leonaspis mutica* (Emmrich). Holotype, HU k195. 1, Dorsal view of the partly enrolled exoskeleton, ×4. 2, Dorsal view of the incomplete free cheek which lies displaced at the side and below the cranidium, ×6.

Figs. 3–8. *Leonaspis crenata* (Emmrich). 3, Lectotype, HU MB 1963/29/1, dorsal view of incomplete cephalon showing the blunt occipital spine, ×4. Mulde Beds, Djupvik in Eksta, Gotland. 4, Oblique dorsal view of incomplete cephalon, RM Ar 30824 showing outline of free cheek and part of librigenal spine, ×8. Mulde Beds (Upper Wenlock), Klintehamn, Gotland. 5, Dorsal view of partly complete cephalon, ×4; locality as fig. 4. 6, Dorsal view of displaced pygidium, RM Ar 31492, ×5; specimen taken without coating of ammonium chloride to show details of the bifid anterior pleural spine; locality as fig. 4. 7, 8, Dorsal and right lateral stereographs of completely enrolled but abraded exoskeleton RM Ar 30806 ×5; note the bifid anterior pleural spine on the third (left) thoracic segment, fig. 7; locality as fig. 4.

Figs. 1–2 taken by Mr. N. Hjorth.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BRUTON, Silurian odontopleurids

*Type localities.* Klintehamn and Djupvik in Eksta, Gotland.

*Horizon.* Uppermost Wenlock, Mulde Beds.

*Description.* Cranidium widest (tr.) opposite the outer ends of S2, from this point tapering slightly anteriorly and posteriorly. Median glabellar lobe flattened to gently arched (tr.), gently convex (sag.); frontal lobe sloping steeply downwards anteriorly (Pl. 32, fig. 8). Frontal lobe short, approximately one-sixth total glabellar length, widening forwards from the inner ends of S2. A change of slope and a broad shallow furrow separates the median glabellar lobe from the occipital ring. Latter short (sag.), moderately convex, with a short, blunt, backwardly curved occipital spine produced from the posterior margin (Pl. 32, figs. 3, 5; Pl. 33, fig. 5). Two pairs lateral glabellar lobes, L1 flattened and weakly convex (tr.), but the posterior half of the lobe slopes steeply downwards to the lateral part of the occipital ring. Beneath the lobe, the outer end of the occipital furrow is very deeply incised. L2 smaller, sub-circular in outline and more convex than L1 (Pl. 32, fig. 8; Pl. 4, fig. 2). S1 transverse to slightly obliquely directed at the outer end, curved inwards and backwards, deep adjacent to the median lobe. The eye ridge runs alongside the outer part of L2 (Pl. 33, fig. 1), becomes straighter opposite S1, and merges with the palpebral lobe which is positioned opposite the outer end of the occipital furrow. Between the eye ridge and the dorsal furrow, is a very narrow (tr.) flattened segment of the fixed cheek which is only slightly wider than the eye ridge. Palpebral lobe (Pl. 33, fig. 1) directed vertically upwards and gently curved outwards at the tip. Eye large, cone-shaped, visual surface with minute eye facets arranged in diagonal lines. Anterior branch of facial suture straight to slightly divergent until it leaves the eye ridge opposite the outer end of S1 and then curving gently inwards to cross the anterior margin in line with the furrow at the base of the palpebral lobe. Antero-lateral margin upturned, outer cheek area very deep at the inner corner below the eye ridge. Posterior branch of suture forming an approximate right angle to anterior branch at the base of eye, from here directed outward and backward in gentle curve before curving strongly backwards inside the base of librigenal spine.

Posterior border curved strongly backwards; border furrow deep at the inner end and beneath eye lobe, becoming shallow to lacking outwards towards the suture. A prominent spine base occurs on the posterior margin just behind the suture (Pl. 33, fig. 5).

Anterior margin of cranidium straight, with single row of tubercle-like spines which increase in size outwards towards the suture (Pl. 33, fig. 1). Outline of free cheek (Pl. 32, fig. 4) resembling a quadrant of a circle, border furrow lacking; a smooth change of slope separates the broad flattened border from the convex part of the cheek (Pl. 33, fig. 2). Margin with twelve short, blunt, fringing spines, the first ten spines from the margin proper, the posterior two spines being at the base of the librigenal spine. Latter slim, round in cross-section, and directed obliquely outwards from a slightly swollen base.

Hypostoma (Pl. 34, figs. 1–2) almost square in outline with a straight to gently curved anterior margin and short, dorsally directed wings. Posterior border flat, lateral corners pointed; posterior margin inclined backwards to small median swelling. Lateral border flat to gently convex, margin sinuous with a small shoulder and a short posterior wing. Anterior lobe of the median body outlined by short, deep triangular middle furrows; posterior lobe broad (tr.), highest point at mid-length, and sloping steeply downwards to the posterior border furrow. Border furrow shallow anteriorly, slightly deepened at

shoulder, defined posteriorly by a change of slope between the posterior lobe and the border. Anterior lobe and border minutely pustulose, posterior lobe smooth (for additional remarks see Lindström 1901, p. 35). The specimen, Plate 34, fig. 2, shows the hypostoma in contact with the rostral plate which is only slightly displaced at the rostral suture. Rostral plate elongated (tr.) and flattened; suture curved, convex forwards medially and sloping outwards laterally. The hypostomal suture is curved to fit the anterior margin of hypostoma. In this position the dorsally directed anterior wing lies beneath the deepened outer part of the anterior border furrow and very near the outer depressed end of the eye ridge. The rostral plate is minutely pustulose.

Exoskeletal surface with very small blunt granules widely scattered over the frontomedian and lateral lobes. The row of short spines on the anterior margin are diagnostic. Free cheeks with close granulation immediately around the eye, remainder of the cheek, occipital ring and furrows, smooth.

Thorax with nine segments (Pl. 32, figs. 7–8). All of the specimens studied are enrolled and except for the first two segments, which are faceted, the pleural spines have been broken. Rachis broad (tr.) moderately convex, and occupying slightly less than half the total pleural width. Lateral shoulders narrow (exs.) directed outwards and forwards where they join the broad, convex principal pleural ridge. Latter curved sharply backwards and swollen at the fulcrum. A shallow pleural furrow separates the principal pleural ridge from the narrow (exs.) raised anterior accessory ridge; the flattened posterior accessory area which is widest (exs.) at the dorsal furrow, narrows outwards and diminishes at the fulcrum. Anterior accessory ridge with a short bifid anterior spine which is directed straight outwards and slightly downwards to lie concealed beneath the fulcrum of the preceding segment. The bifid spine is just visible on the third (left) segment of the specimen (Pl. 32, fig. 7). The spine is absent on the first segment of the thorax. On enrolled specimens, the first two segments are shortened, curved backwards, and tucked under the posterior margin and inside the base of librigenal spine. Rachis apparently smooth, but one conspicuous short tubercle is situated on each pleuron just inside the fulcral swelling.

Pygidium (Pl. 32, figs. 6, 7) similar to that described for *Leonaspis angelini* (Pl. 34, fig. 4) but differing in having a broad, shallow dorsal furrow and a wider (tr.) pleural area which has a bifid spine at the antero-lateral corner. This structure corresponds to that seen on the thoracic pleura and is only visible when the pygidium is displaced as in Plate 32, fig. 6. Whittington (1956*b*, pp. 508–9, pl. 57, fig. 9) described a similar structure on the pleura and pygidium of *L. tuberculatus* (Hall 1859).

It seems reasonable to assume that the most anterior point of the spine represents an

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EXPLANATION OF PLATE 33

Figs. 1–2, 5. *Leonaspis crenata* (Emmrich). 1–2, Anterior and oblique left lateral stereographs of enrolled exoskeleton, RM Ar 30809, ×4½; note the directions of facial sutures, shape of eye lobe, and curved outer lip of palpebral lobe. 5, Anterior view of incomplete cephalon RM Ar 31492, showing the blunt occipital spine, ×4½. Mulde Beds (Upper Wenlock), Djupvik in Eksta, Gotland.

Figs. 3–4, 6, 7. *Leonaspis muldensis* sp. nov. 3–4, Holotype, dorsal stereograph and anterior view of incomplete, worn exoskeleton, RM Ar 30826, ×4½. 6, Small enrolled individual, RM Ar 30826/1, showing how the pleural spines fit inside edge of the free cheek, ×6. 7, Worn thorax and pygidium RM Ar 47405, ×6. All specimens from Mulde Beds, Djupvik in Eksta, Gotland.

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BRUTON, Silurian odontopleurids

articulating process, while the posterior point is homologous with the anterior spine commonly found on other odontopleurid pleurae.

*Discussion.* Emmrich named and briefly described this species in the programme of 'Realschule in Meiningen' 1844. An exact reprint of this paper appeared in the *Neues Jahrbuch* for 1845. No figures were given. For this reason, there is a little doubt whether the specimen here designated as lectotype was available to Emmrich when he gave the original diagnosis of the species. However, Dr. Hermann Jaeger (personal communication 9. 10. 63) believes that the specimen belonged to Emmrich's collection. The specimen is labelled as coming from Klintehamn, Gotland, which locality, Dr. Anders Martinsson informs me, is the nearest point of habitation to the type locality of the Mulde Marl. All specimens of *L. crenata* which I have examined, in Swedish museums have been collected from the Mulde Marl at Djupvik in Eksta.

Lovén (1845, p. 47, pl. 1, figs. 6*a–b*) gave a complete description of this species and was the first to figure specimens. The description and the figures were considerably more accurate than the idealized illustration given by Angelin (1854, pl. 21, figs. 6*a–b*). The specimens of these two authors have not been identified in the Riksmuseum Collections.

The specimens from Britain described as *Acidaspis crenata* by Lake (1896, pp. 239–40, pl. 7, figs. 1, 2) are very similar to the Swedish species but differ in details of the pygidium and exoskeletal ornament. In a forthcoming paper I intend to redescribe the British material as a new species.

*L. crenata* resembles *L. tuberculatus* (Hall) and *L. williamsi* (cf. Whittington 1956*b*, pp. 507–10, pl. 57; pl. 58, figs. 1–7) but appears closer to the second species which has a similar type of pygidium and free cheek; the occipital ring has a short blunt spine. *L. crenata*, however, has a hypostoma, approximating more closely to a square, a less strongly decorated exoskeleton, and a greater number (9) of thoracic segments.

### *Leonaspis muldensis* sp. nov.

Plate 33, figs. 3–4, 6–7

*Derivation of name.* From *Mulde*, the name of the type horizon.

*Holotype.* The enrolled cephalon and thorax (RM Ar 30826) figured as Plate 33, figs. 3–4.

*Other material.* One incomplete thorax and pygidium (RM Ar 47405) and one enrolled cephalon and thorax (RM Ar 30826/1).

*Dimensions of holotype.* Length of cranidium 4·7 mm.; width between palpebral lobes 6·5 mm.

*Type locality.* Djupvik in the parish of Eksta, Gotland.

*Horizon.* Uppermost Wenlock, Mulde Beds.

*Diagnosis and description.* Three enrolled specimens, which differ considerably from *L. crenata*, have been found among a large sample of *L. crenata* from the Mulde Marl. These specimens are here described as the new species *L. muldensis*.

When sorting the material, *L. muldensis* is easily distinguished from *L. crenata* on account of the more compact form of spheroidal enrollment which is a reflection of the wider (tr.) and less tapered thorax. Other important differences may be described as follows: Cranidium (Pl. 33, fig. 3) approximately one and a half times as wide as long, with the occipital ring lacking the blunt median spine; anterior margin straight and

without the single row of small spines; palpebral more widely spaced and shorter; eye ridge concomitantly more divergent with a wider (tr.) posterior part of the fixed cheek. The anterior branch of the facial suture curves more strongly inwards anteriorly and the antero-lateral part of the border is strongly upturned and very deep. Free cheek with narrow convex border and deep furrow inside the anterior suture, furrow becoming shallower towards base of librigenal spine and the border is wide and flattened. Cheek margin curved steeply outwards and downwards (Pl. 33, fig. 4), so that when the specimen is viewed dorsally (Pl. 33, fig. 3), the short fringing spines are scarcely visible. Librigenal spine and hypostoma not known.

Thorax (Pl. 33, figs. 6–7) with ten segments, of which only the first appears to be shortened (tr.). Principal pleural spines less stout, and fulcral swelling not obvious.

Pygidium (Pl. 33, fig. 7) only known from one rather worn specimen but, nevertheless, very different from that of *L. crenata*. Outline rectangular, slightly less than four times as wide as long. Rachis tapering backwards, with convex first ring, and a smaller second ring with short terminal portion. Dorsal furrow short and pit-like alongside the second ring but apparently dying out posteriorly. The narrow pleural ridge diverges outwards and backwards and reaches the posterior border at approximately one-half pleural width. Only the bases of four inner secondary spines are visible, while there is one short outer secondary spine. The specimens are all rather water-worn and the surface granulation, with the exception of a transverse row on the frontal glabellar lobe, is not preserved.

*Discussion.* The shape of the pygidium shows that *L. muldensis* is possibly related to *L. marklini* and *L. mutica*. The presence of ten thoracic segments and traces of a coarse granulation, on what is otherwise a badly worn specimen, suggests an affinity with *L. marklini*. The broad, downwardly curved free cheek border and the ventrally directed fringing spines, are features which enable the free cheek of *L. muldensis* to be separated from that of *L. marklini* and *L. mutica*.

### *Leonaspis angelini* (Prantl and Přibyl, 1949)

Plate 34, figs. 3–6

1854 *Acidaspis Barraudei* Angelin, p. 38, pl. 22, fig. 14.
1885 *Acidaspis barrandei* Angelin; Lindström, p. 53.
1949 *Acanthaloma angelini* Prantl and Přibyl, pp. 159–60, pl. 10, figs. 11–12.

*Holotype.* The almost complete specimen (RM Ar 30859), figured by Angelin 1854, pl. 22, fig. 14, and refigured herein as Plate 34, figs. 4–6.

*Material.* In addition to the holotype, one fragmentary free cheek (RM Ar 47407).

*Dimensions of holotype.* Length of cranidium (projected) 3·5 mm.; width of cranidium 5·8 mm.; width

EXPLANATION OF PLATE 34

Figs. 1–2. *Leonaspis crenata* (Emmrich). 1, Dorsal stereograph of hypostoma and damaged rostral plate RM Ar 30816, original of Lindström 1901, pl. 1, figs. 3–6, ×10. 2, Slightly damaged hypostoma in contact with rostral plate RM Ar 30813, ×9. Mulde Beds, Djupvik in Eksta, Gotland.

Figs. 3–6. *Leonaspis angelini* (Prantl and Přibyl) (ex. *barraudei* Angelin). 3, Ventral view of incomplete free cheek RM Ar 47407, ×7. 4–6, Holotype RM Ar 30859, the original of Angelin 1854, pl. 22, fig. 14. 4, Dorsal stereograph of complete exoskeleton, ×2. 5, 6, Anterior and oblique left lateral views, ×2. Slite Beds (lower Upper Wenlock), Lilla Karlsö, Gotland.

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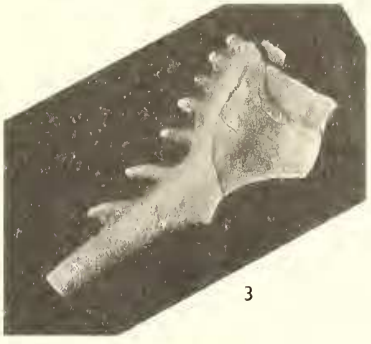

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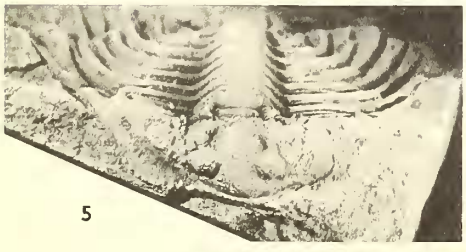

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BRUTON, Silurian odontopleurids

of cephalon 11 mm. approx.; width of thorax at first seg. 9·5 mm.; width of thorax at ninth seg. 5·5 mm.; length of thorax 9 mm.; width of pygidium 4·? mm.; length of pygidium 1·5 mm.

*Type locality*. Lilla Karlsö, Gotland.

*Horizon*. Lower–Upper Wenlock, Slite Beds.

*Description*. The cranidium of the holotype has been pressed inwards and partly crushed on the right-hand side and the free cheek has been slightly displaced. Median glabellar lobe broad and flattened (tr. and sag.), parallel-sided as far as inner ends of S2, then widening forwards to give flattened frontal lobe. The occipital ring is broken in its mid-part so that here details are not known. Outer part of occipital furrow considerably deepened beneath L1, and a small tubercle is present in place of an occipital lobe. Two pairs of lateral lobes, L1 the larger, sub-oval in outline but rather pointed at the outer end. L2 small and globose. S1 curved sharply inwards, the inner end deep and parallel with the otherwise shallow longitudinal furrow. S2 directed more obliquely inwards from inside the eye ridge. Latter very weakly convex, curves outwards around L2 and then becomes straighter. A small broken part of the palpebral lobe indicates that the eye was positioned well backwards opposite the base of L1, and was directed upwards off the highest part of the cheek. Fixed cheek a very narrow ornamented band which slopes steeply inwards alongside the posterior half of L1. Anterior facial suture not clearly visible, but apparently directed straight forwards from base of eye and then gently curving inwards and crossing the anterior border in line with the dorsal furrow. Posterior branch of suture directed outwards, at right angles to the anterior branch, curved forwards in a gentle convex curve, then turned backwards distally inside the librigenal spine. Posterior border with a prominent spine base just behind the suture.

Free cheek sub-quadrate and tapering backwards towards the librigenal spine. Border broad and flattened near the anterior suture but more convex with deepened border furrow at the base of the librigenal spine. Latter slim, oval in cross-section. The border spines, of which there are at least ten, increase in length backwards and the most posterior two spines occur at the base and along the outer edge of the librigenal spine (Pl. 34, fig. 3). Cheek surface and border coarsely granular, the librigenal spine and the fringing spines of the cheek finely granular. Thorax of nine segments, of which the first two are shortened transversely. On the holotype (Pl. 34, fig. 4) the first segment is partly hidden beneath the backward sweep of the posterior margin because of the tilting of the cephalon relative to the thorax. Rachis wide (tr.), moderately convex, occupying slightly more than one-third the total pleural width. Principal pleural ridge strongly convex, slightly swollen at the fulcrum. Principal pleural spines long, tapered, directed slightly downwards and then curved strongly backwards sub-parallel to each other. Principal pleural ridge separated by change of slope from the narrow (exs.) raised anterior accessory ridge which has a small articulating process at the fulcrum but no true anterior spine. Rachial rings each with a pair of conspicuous tubercles positioned on the lateral parts and smaller scattered granules elsewhere. Principal pleural ridge also with small tubercles positioned just inside the fulcral swelling and at approximately one-third pleural width (from rachis). Anterior accessory ridge with single row of very small granules. Remainder of exoskeleton, including pleural spines, minutely pustulose.

Pygidium with narrow, moderately convex first rachial ring connected by a very short pleural ridge to the long, slim, backwardly directed major spines. Latter approximately

three times the total length of the pygidium. Posterior border connected to the inner parts of the major spines so that a raised ring surrounds the second rachial ring. Latter vaulted by reason of the deep dorsal furrows which circumscribe all but the tip of the rachis. Between the major spines a pair of short slim spines directed horizontally backwards. Outer pleural area short (tr.) and ear-like with single row of small tubercles directed obliquely across the surface to the base of the single anterior secondary border spine. Pleural ridge with prominent tubercle at the base of the major spine, rachial rings finely granular but each with a pair of conspicuous tubercles; remainder of surface minutely papillate.

*Discussion.* Prantl and Přibyl (1949, pp. 159–60) quite correctly recognized that the species name *Acidaspis barrandei* Angelin 1854, as applied to a species of *Leonaspis*, was a junior primary homonym of the older British name *Acidaspis barrandii* Fletcher-Salter 1853, applied to a species of *Ceratocephala*. In consequence, the new name *angelini* Prantl and Přibyl 1949, was established for *barrandei* Angelin.

Much of the confusion relating to the priority of the two species names had arisen because of the belief that the British species was still a manuscript name after the publication of Angelin's work. Lindström (1885, p. 53) believed this to be the case but Lake (1896, pp. 241–2) correctly outlined evidence to the contrary. The history of the name is as follows:

Salter (1848, p. 349, pl. 9, fig. 4) figured a cephalon from the Wenlock Limestone, Dudley, under the name *Acidaspis bispinosus* M'Coy, but remarked that this, and other specimens from the same locality, were longer and possessed a different glabella convexity from the type of M'Coy. Later, Salter (1853, p. 6) noted that the specimen was not conspecific with M'Coy's type as at first inadvertently thought, and he said that the form had been named *Acidaspis Barrandii* by Fletcher and was to be described shortly. The species was later refigured in Murchison's 'Siluria' 3rd, edn. 1859, but no full description appeared until the work of Lake (1896, p. 241, pl. 8, figs. 1–3).

Succeeding authors, Lake (loc. cit.); Reed (1906, p. 112); Prantl and Pribyl (1949, p. 160) and others, attributed this species name to either Fletcher and Salter or Salter. The correct quotation should be *barrandii* Fletcher in Salter 1853 (see I.C.Z.N. **51** (*c*)). From 1853 onwards, the name was in current use in Britain (see Lake 1896, p. 242) and was perfectly valid despite the fact that it was quoted erroneously by Morris (1854, p. 98), as being a manuscript name. Lindström (1885, p. 53) believed the first use of the name for the British species was by Morris and therefore thought that the Swedish name had priority since the work of Angelin, published in the early part of 1854, appeared before Morris's catalogue which was printed in July.

For the reasons outlined above, the British species name was already valid in 1853.

Lindström (1885, p. 54) noticed the resemblance between the pygidium of *L. angelini* and *L. crenata*. In *L. angelini*, however, the major border spine and pleural ridge occupies almost the entire width of the pleural area and there is no bifid anterior border spine. The free cheek of *L. crenata* can be distinguished from that of *L. angelini* on account of the broad, flattened, and smooth border, and the shorter peg-like fringing spines.

Angelin (1854, pl. 22, fig. 14) illustrated paired tubercles on the occipital ring, but this part has since been broken. If there are paired tubercles on this part, cranidia of *L. angelini* can be readily separated from *L. crenata* because the latter has a short spine on the occipital ring.

*Leonaspis varbolensis* sp. nov.

Plate 35, figs. 1–2, 4

? 1938 *Leonaspis marklini* (Angelin); Whittard, p. 108, pl. 3, fig. 14.

*Derivation of name.* From the name of the type locality.

*Holotype.* The cranidium with a damaged occipital ring (EA Tr 1802/1) figured as Plate 35, fig. 2.

*Dimensions of holotype.* Length of cranidium 3·5 mm.; width (measured across the palpebral lobes) 4 mm.

*Type locality.* Varbola well, Estonia.

*Horizon.* Lowermost Llandovery, Juuru Stage ($G_1$).

*Material.* In addition to the holotype, one free cheek and two cranidia (EA Tr 1802/2–4) from the type locality; two cranidia, one fragmentary free cheek, and four pygidia (EA Tr 2239/1–7) from the Llandoverian Rastrites Shale, Engure Boring (level 857–1003 m.), Piltene, Latvia; one cranidium (GSM 55482) from the Llandoverian Pentamerus Beds, Shineton, Shropshire, which was figured by Whittard 1938, pl. 3, fig. 14.

*Diagnosis and description.* Cranidium (Pl. 35, fig. 2) with the maximum length (sag.) slightly less than maximum width. Median glabellar lobe outlined by the deep longitudinal furrows and maximum transverse width level with the inner end of S1. From this point, the anterior section of the longitudinal furrow is curved in a bow-shape inwards, while the posterior section is straight and converges backwards; transverse width of median lobe in front of the occipital furrow about two-thirds the maximum width. Frontal lobe with a rounded outline, sloping steeply down to the anterior border furrow. The occipital ring is about four times as wide as long and is gently convex. Two pairs of lateral lobes; L1 oval in outline, about half as long as the fronto-median lobe with the longest axis exsagittal; L2 about half the size of L1 with the longest axis oblique to the sagittal line. S1 deep between the lobes, inclined at about 20° and then curved backwards parallel to the longitudinal furrow; S2 inclined more steeply inwards. Palpebral lobe positioned far backwards on a transverse line drawn through the midpart of L1; lobe directed upwards and backwards, lip curved outwards. Fixed cheek a narrow, gently convex area with the maximum width inside the palpebral lobe slightly less than the width of L1; cheek curves strongly downwards posteriorly from the highest point which is level with the anterior one-third of L1. Anterior branch of the facial suture leaves the eye ridge opposite the highest part of the fixed cheek and runs forward, only slightly convergently, and crosses the anterior margin at a point on an exsagittal line drawn through the midpart of the fixed cheek. Antero-lateral triangle of outer fixed cheek broad and flattened but slightly deepened at the inner corner. Posterior branch of suture directed outwards at right angles to the anterior suture and slanting backwards before turning abruptly backwards inside the base of the librigenal spine. Transverse width of the posterior border equal to one-half the width of the cranidium. Fronto-median lobe, lateral lobes, fixed cheek, and occipital ring with large blunt tubercles which are very closely spaced; anterior border minutely granulated, furrows smooth. The cranidium of Plate 35, fig. 1 is preserved as an internal mould in shale and the exoskeleton is not preserved.

Only one poorly preserved free cheek, exposed from the ventral side, is known from the type locality. The base of the librigenal spine is broad and there are thirteen fringing spines. No pygidia are known from the type locality, but the specimen (Pl. 35, fig. 4) which was found with the cranidium (Pl. 35, fig. 1) at an approximately equivalent horizon in Latvia, is assumed to belong here. The pygidium, which is preserved as an internal mould, is exceedingly like the pygidium of *L. marklini* (Pl. 30, fig. 5.)

*Discussion.* The cranidium of *L. varbolensis* (Pl. 35, fig. 2) is like that of the younger *L. marklini* (Pl. 30, fig. 4; Pl. 31, fig. 3), but differs mainly in the outline of the median glabellar lobe, the less anteriorly pointed L1, the straighter, less convergent anterior branch of the facial suture, and the more closely spaced granulation on all parts of the cranidium. The latter feature and the smooth anterior margin of the cranidium, serve to separate *L. varbolensis* from *L. centrina* (Pl. 35, fig. 12). In my opinion, the cranidium figured by Whittard (1938, pl. 3, fig. 14) is closer to *L. varbolensis* than it is to *L. marklini* with regard to the straighter anterior branch of the facial suture and the outline of the median glabellar lobe. However, the occipital ring of the English specimen is longer (sag.) and more convex in its median part and the surface granulation, although as coarse as in *L. varbolensis*, is less closely spaced on the fronto-median glabellar lobe.

### *Leonaspis centrina* (Dalman, 1828)

Plate 35, figs. 11–12; text-fig. 1

1828 *Calymene centrina* Dalman, p. 35.
1844 *Odontopleura centrina* (Dalman); Emmrich, p. 17.
1845 *Odontopleura centrina* (Dalman); Emmrich, p. 44.
1845 *Calymene? centrina* (Dalman); Lovén, p. 48.
1854 *Acidaspis granulata* (Wahlenberg); Angelin, p. 37, pl. 22, fig. 11.
1869 *Acidaspis centrina* (Dalman); Linnarsson (*partim*), p. 65.
1896 *Acidaspis centrina* (Dalman); Lake, p. 224.
1921 *Acidaspis centrina* (Dalman); Troedsson (*partim*), pp. 4, 6, 10, tab. p. 12.
1938 *Acidaspis centrina* (Dalman); Whittard, p. 107.
1948 *Leonaspis centrina* (Dalman); Wærn, p. 461.
1960 *Leonaspis centrina* (Dalman); Kielan, p. 101, pl. 15, fig. 5, text-fig. 26.
1966*b* *Leonaspis centrina* (Dalman); Bruton, pp. 10–11.

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EXPLANATION OF PLATE 35

Figs. 1, 2, 4. *Leonaspis varbolensis* sp. nov. 1, Internal mould of cranidium EA Tr 2239/1, dorsal view, ×5. 4, Internal mould of pygidium, EA Tr 2239/2, ×4. Rastrites Shale (Lower Llandovery), level 1003·05 m., Piltene boring, Latvia. 2, Holotype, EA Tr 1802/1, dorsal view of cranidium with damaged occipital ring, ×7. Juuru Stage ($G_1$), Lowermost Llandovery, Varbola well, Estonia.

Figs. 3, 5, 6. *Acidaspis pectinata* Angelin. 3, Incomplete free cheek and part-cranidium, RM Ar 30876, dorsal view, ×1½. Lowermost Högklint Beds (above Llandovery–Wenlock boundary), 'Visby-b', Gotland. 5, Incomplete pygidium exposed from the ventral side, RM Ar 30865, ×2. 6, Internal mould of free cheek and incomplete cranidium in dorsal view, RM Ar 30867, ×1½. ?Upper Högklint Beds, 'Visby-b', Gotland.

Figs. 7–9. *Anacaenaspis* aff. *A. gotlandensis* gen. et sp. nov. 7, 8, Latex cast of external mould of incomplete cephalon, RM Ar 30817/1, oblique right lateral and dorsal views, ×3. 9, Internal mould of the pygidium seen lying alongside the cephalon in fig. 8, RM Ar 30817/2, ×4. Gotland, horizon and locality unknown.

Fig. 10. *Anacaenaspis gotlandensis* gen. et sp. nov. Damaged cephalon exposed from the ventral side, RM Ar 30806a, ×2. Uppermost Hemse Beds (Middle Ludlow), Lau Kanal, Gotland.

Figs. 11–12. *Leonaspis centrina* (Dalman). 11, Partly compressed pygidium, UM Vg 806, ×10. Lower Llandovery, level 22·20 m., Kullatorp bore, Kinnekulle, Västergötland. 12, Cranidium, UM Vg 805a, dorsal view, ×10. Level 25·70 m. of the same bore core. Wærn Collection 1948.

Fig. 13. *?Acidaspis* sp. indet. Incomplete pygidium EA Tr 1844/4, exposed from the ventral side, ×3. Adavere Stage ($H_4$), Upper Llandovery, River Velise i Voiva, Estonia. Coll. R. Männil.

Fig. 14. *Anacaenaspis emarginata* (Schmidt). Holotype, KML 17857, the original of Schmidt 1885, pl. 1, fig. 1, incomplete cephalon, oblique left lateral view, ×3. Jaani Stage ($J_1$), Koguva säär, Island of Muhu, Estonia.

Figs. 11–12 taken by Mr. N. Hjorth.


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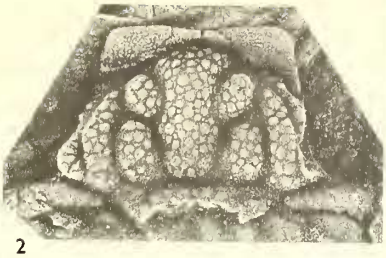
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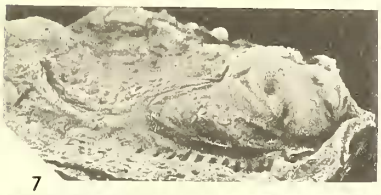
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BRUTON, Silurian odontopleurids